

THE LIFE HISTORY OF *YLLENUS ARENARIUS* (ARANEAE, SALTICIDAE)—EVIDENCE FOR SYMPATRIC POPULATIONS ISOLATED BY THE YEAR OF MATURATION

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ABSTRACT. The lifespan of *Y. arenarius* is about 720 days for males and 750 days for females (maximum 770 days), which makes it the longest lived salticid reported from natural conditions. The juvenile spiders emerge at the beginning of June and mature not before the following August. They mate in autumn and hibernate for the second time. For most of the year two cohorts coexist, and at the beginning of June three cohorts can be found simultaneously. The life cycle suggests that in the studied areas there are two groups of individuals, the first of which produces young in odd years, while the other group reproduces in even years. The spider lifespan and phenology suggest no or limited gene flow between the groups.

Keywords: Salticidae, life history, sympatric populations, isolation, *Yllenus arenarius*

Spider life histories have received considerable attention, which has led to some general attempts at life cycle classification and understanding the factors responsible for cycle control, and for growth and development of spiders (rev. in Schaefer 1987; Vollrath 1987). The specific knowledge of life cycles is, however, restricted to some groups, while others remain poorly known.

The knowledge of salticid life cycles is very scarce. The spiders are relatively small and occur in low densities, so they have attracted little interest concerning both general biology and ecology (Wise 1993). Since the works published by the end of the seventies (e.g.: Horner & Starks 1972; Edwards 1975; Jackson 1978) few papers on the topic have appeared (e.g.: Matsumoto & Chikuni 1987). Instead, salticids have recently been the subject of intensive behavioral studies (rev. in Jackson & Pollard 1996) and some species have gradually become models in studies of invertebrate cognition (e.g.: Wilcox & Jackson 1998). The knowledge of the model's general biology is often, however, essential for the proper interpretation of ecological and behavioral data.

Jumping spiders are commonly characterized as possessing stenochronous life cycles (Schaefer 1987). From particular studies car-

ried out on species occurring in temperate climate we know that they have annual or biennial life cycles (e.g.: Horner & Starks 1972; Jackson 1978; Matsumoto & Chikuni 1987). Such information can also be deduced from the occurrence of sexually mature individuals, which is sometimes given in local keys (Prószyński 1991).

The current work aims to describe the life history of *Yllenus arenarius* Menge 1868, which is a medium-sized jumping spider with an adult body length of about 7 mm. Typically for Salticidae, sexual dimorphism is poorly marked in body size but distinct differences are exhibited in coloration. It is known only from Central and Eastern Europe with the westernmost localities in NW Germany and the easternmost on the river Volga (Prószyński 1991; Logunov & Marusik 2003). The spider inhabits sandy dunes along rivers as well as inland and coastal dunes. In the habitats it is restricted to the initial stage of the *Spergulo-Corynephorum* and tends to keep away from dense vegetation (Żabka 1997; Bartos 2000; Merckens 2002).

Yllenus arenarius is a polyphagous salticid preying on a wide spectrum of invertebrates (Bartos 2004). It is also known for its conditional hunting tactics flexibly adjusted to prey type (Bartos 2000, 2002a). Another interesting

fact concerning the spider's biology is its unusual sub-sand nests built for various purposes: molting, egg-laying, surviving the period of night and hibernating. The nest types differ according to their size, shape and general structure (Bartos 2002b).

METHODS

Study period and area.—The research carried out from 1998–2003 encompassed 14 populations from Central and Eastern Poland. One of the sites (Kwilno), located in Central Poland about 25 km to the north of Lodz, was visited at least every two weeks during the vegetation season. Data from the other sites were collected more occasionally, but with respect to spider phenology and body size they were consistent with the data from Kwilno and therefore they were pooled.

Morphometric measurements and phenology.—Spiders were collected by means of visual searching through the dune surface between 10:00 and 12:00 hours. During each field visit it was attempted to collect at least 40 individuals (10 juveniles from each cohort, 10 females and 10 males). Spiders from all age groups show the same pattern of variation in activity during the day, therefore the samples seem to be representative for the whole population (Bartos pers. obs.). In anticipation of hatched juveniles or adults after the final molt the field was visited every day starting at least ten days before the expected time.

Three measurements of live specimens were taken with a stereomicroscope (precision: 0.01 mm) ($n = 1208$): abdomen length (AL), abdomen width (AW) and posterior eyes width (PEW). To immobilize the spiders during the measurements they were covered with a transparent kitchen foil and delicately pressed against a piece of sponge. Sex and age of the spiders were also recorded. The characteristics allowed to include the spiders to certain age groups (Figs. 1–3).

Winter samples.—In winter a two-centimeter thick layer of sand was collected from the dune surface and dried in the laboratory (temperature at ca 25 °C). Spiders, which emerged from the sand were collected, measured and subsequently reared until they died. The dried sand was also sieved to collect nests and immersed spiders. Air temperature at the level of the sand surface was measured with an alcohol thermometer (precision: 0.2 °C).

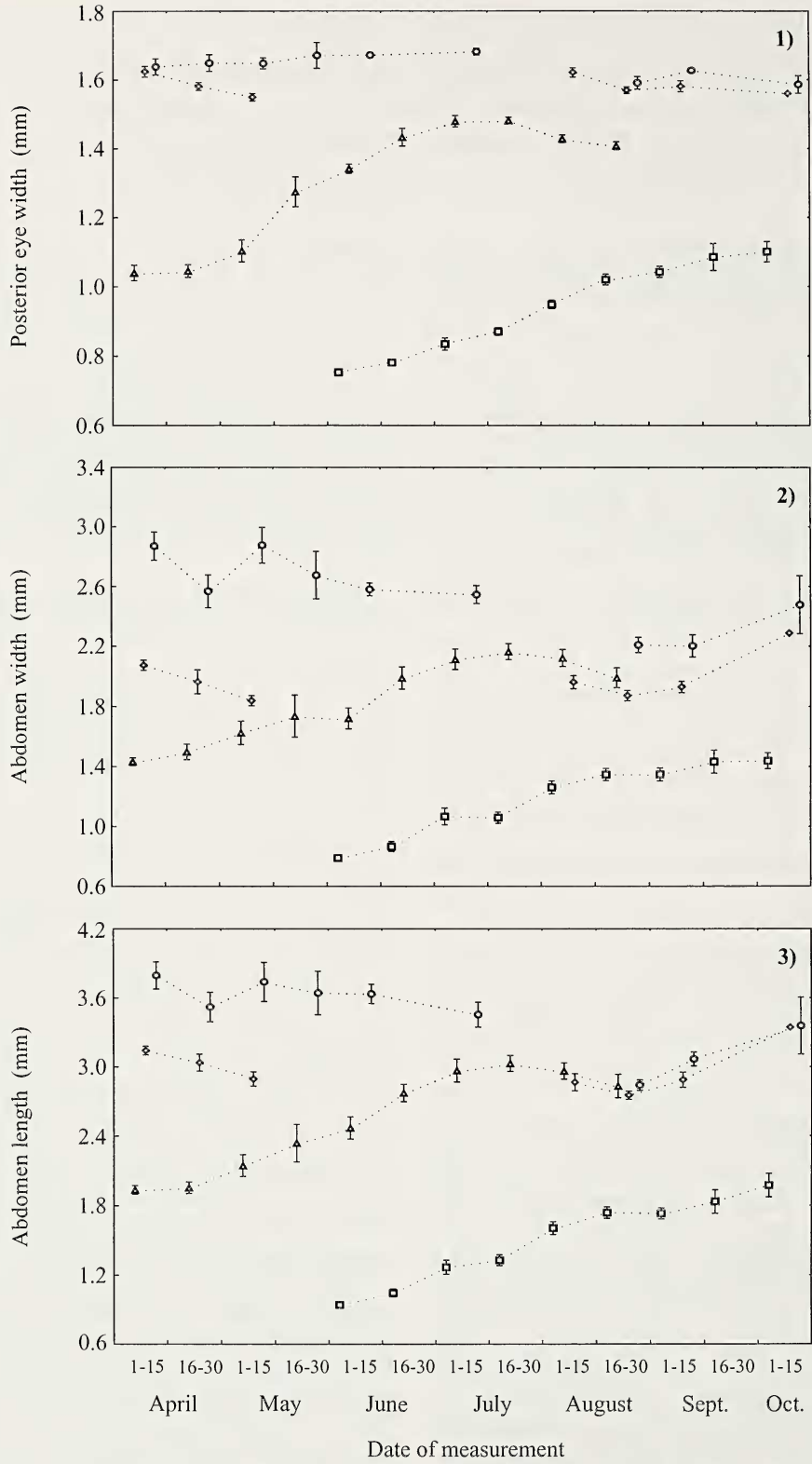
Rearing.—Females were kept in the laboratory to estimate the number of eggs, the period of egg laying and determine the place where they are laid. Spiders were reared individually in glass containers (1 liter) with a three centimeter-thick layer of dune sand on the bottom. Temperature was maintained at ca 25 °C, light regime 12L:12D and the sand was moistened weekly with 5 ml of water. They were fed ad libitum (10 fruit flies twice a week). Under these conditions 26 females were kept. Six females came from winter sand samples and the rearing started in February, while 20 other females were collected at the beginning of April. The sand from the laboratory containers was sieved every two weeks in order to collect nests. The nests were opened and checked to find eggs and exuviae. The individuals in the laboratory survived until mid June.

Data analysis.—All statistical procedures followed those described by Zar (1984). The significance of the differences in body length parameters was tested with one-way ANOVA and Tukey test with unequal sample sizes. Data are presented as mean \pm SD (n) except for Figs. 1–3 which present mean \pm 1.96 SE.

RESULTS

Morphometric measurements and phenology.—Taking into account the season in which the spiders were collected, spider size and maturity, four age groups were distinguished (Figs. 1–3): juveniles in the first season of life (juv-I), juveniles in the second season of life (juv-II), which underwent maturation in August, adults in the second season of life (ad-II) and adults in the third season of life (ad-III). In each of the studied seasons two spider cohorts were observed for the whole season (either juv-II and ad-III or juv-I and juv-II/ad-II) and, in June, spiders from all three cohorts were observed simultaneously (juv-I, juv-II and ad-III).

Spiders from the same cohort were observed for three consecutive years (Figs. 1–4). Males were found even up to 720 days from leaving their sub-sand nests. The latest recording time for females ($n = 3$) was 15 July in 1998 and 2003. Their lifespan, calculated from the time of emerging from the sub-sand nest, is about 750 days. The females, however, were numerous only by the begin-



Figures 1–3.—Changes of three morphometric parameters in the life cycle of *Yllenus arenarius*. 1. Posterior eyes width; 2. Abdomen width; 3. Abdomen length; squares, juv-I ($n = 573$); triangles, juv-II ($n = 363$); diamonds, males ($n = 124$); circles, females ($n = 148$); symbols are means; error bars are 1.96 SE.

ning of June. Later only scattered individuals were recorded.

Spiders of all age groups were active from the first 10 days of April to mid October as long as the air temperature measured on the dune surface was above ca 10 °C. Spiders were never found when the temperature was lower than 10 °C. Therefore, because of overall harsh autumn weather conditions, in most seasons of study they disappeared before the end of September, rarely at the beginning of October (Figs. 1–3). On several warm winter days in February, however, several females were found hunting on the dune surface (at temperature 11.4 °C). All age groups started their activity at the same time in spring and were also found to burrow almost simultaneously for hibernation in autumn.

Juveniles in the first season of life (juv-I): During three study seasons, when the newly emerged juveniles were searched for, they appeared within almost the same period of time (between 3 and 6 June). Their body length was about 1.87 ± 0.14 mm ($n = 30$), they had semitransparent carapace and their round cephalothorax and abdomen closely resembled the dune sand grains in color, size and shape. Shortly after emergence the spiderlings were found in groups of up to six individuals remaining only a few meters from each other, which suggests that they emerged from the same sac. Later, when the spiders started to disperse, they were rather evenly distributed over the dune. However, even a week after the first juveniles appeared on the surface, some groups consisting of a few spiderlings were also found, which suggests that they had just left the hatching chamber. Juveniles in the first season of life were observed throughout the summer until the beginning of October, when the first hibernation started (Figs. 1–3).

Juveniles in the second season of life (juv-II): The spiders finished their hibernation at the beginning of April. In mid June the distal parts of the pedipalps of some juveniles began to swell, which made it easy to determine them as subadult males. They reached the subadult stage at different times and swollen pedipalps were commonly observed in subadult males only in mid July. Other characteristics of both sexes prior to final molting were indistinguishable. Spider color and body pattern, so different in adult males and females, were identical in subadults. In the last week of July

almost all juveniles in the second season of life burrowed to undergo the final molt in their sub-sand nests. The first to disappear, however, were subadult males. At that period only juv-I were commonly found on the surface. Such pattern of simultaneous disappearing of almost all individuals from a cohort, while the other cohort did not show apparent differences in number, was observed several times in the field. However, such absence was recorded for only a few days, which cannot be presented in the two-week-long periods in the figures.

Adult spiders: The first adults to appear were males, observed as early as 8 August. During all three years, when the first mature males were particularly searched for, they appeared regularly between 8–10 August. The first adult females were observed at least ten days later. Male coloration and body pattern changed significantly after the last molt. Generally, after the last molt males became much more conspicuous and easy to spot while female cryptic coloration remained unchanged. Female coloration also changed throughout their mature life mainly due to losing scales in the course of burrowing. In June, i.e. after 10 months from the last molt they were much darker, with patches of black cuticle visible in the areas where the scales were missing. In extreme cases the dorsal area of their abdomen was black. This makes them unmistakable from freshly molted females.

Not only general appearance, but also some body measurements of adult females changed over their mature life (Figs. 1–3). There were no differences in posterior eyes width (Fig. 1) ($F_{8;143} = 1.38$, $P > 0.05$). Such differences were found, however, for abdomen length ($F_{9;137} = 4.89$, $P < 0.001$) and abdomen width ($F_{9;139} = 5.71$, $P < 0.001$). Freshly molted adult females had on average shorter abdomens than those in the next spring by the end of May (significant at $P < 0.05$), but not the females in the second half of April ($P > 0.05$). A similar tendency was observed for abdomen width, being thinner in females shortly after the final molt in comparison with those in the first half of April and in the first half of May ($P < 0.05$), but again no differences with females in the second half of April. The latter group had on average shorter abdomens than the females directly before and after the period ($P < 0.05$).

In the group of adult males the differences

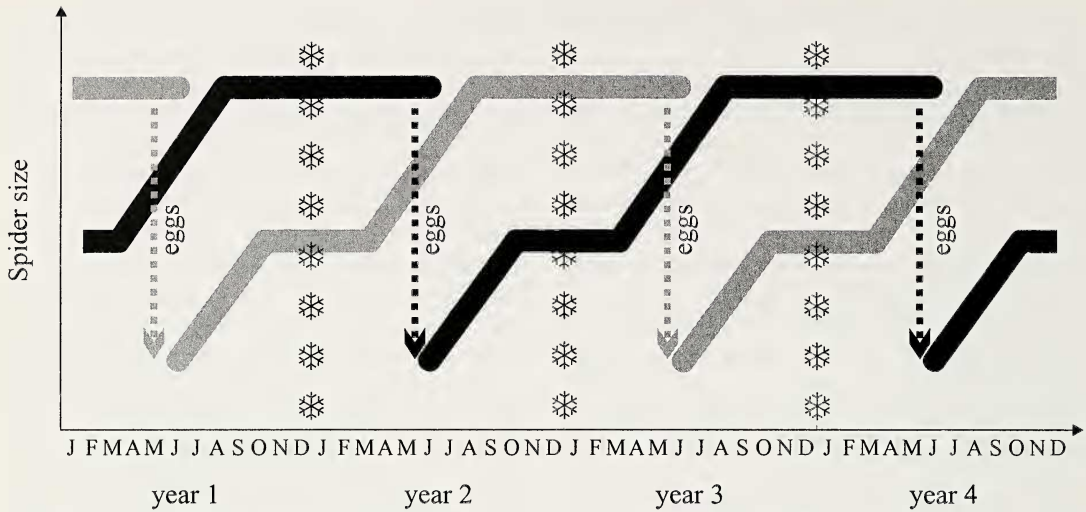


Figure 4.—Schematic presentation of the life cycle of *Yllenus arenarius*. grey bars = spiders hatching in odd years; black bars = spiders hatching in even years.

were found only between those measured in the second half of August and early next spring. The first group was larger than the second according to posterior eyes width ($F_{6,121} = 3.01, P < 0.01$) (significant at $P < 0.05$), abdomen length ($F_{6,109} = 8.38, P < 0.001$) ($P < 0.001$) and abdomen width ($F_{6,109} = 4.17, P < 0.001$) ($P < 0.005$).

Winter samples.—In winter sand samples collected in February at ambient temperature of -8°C and under ten-centimeter-thick snow cover, 26 live individuals were found. These were juv-II ($n = 12$), ad-III ($n = 14$): eight males and six females. Spiders from all age groups hibernated successfully. Spiders were found in only one out of four sand samples. Two spiders were found in elongated nests impregnated with organic matter, while the other individuals were being active at the time and were collected from the sand surface. Their winter nests were found after sieving the sand.

Rearing.—Females reared in the laboratory ($n = 26$) laid on average 6 ± 0.8 eggs ($n = 5$). The eggs were spherical or slightly oval, on average 1.20 mm in diameter ($\text{SD} = 0.17$ mm, $n = 4$). In all cases the eggs were laid in one batch only. The nest in which eggs were laid was different from other nests found in the same container. It possessed a specific structure. It was made of dense silk and sand grains and possessed two chambers. Eggs were attached to the wall with a sheet of silk slightly pressing them to the wall. Inside, the

eggs and empty chorions were found. The spiderlings hatched in a small chamber of the nest, and molted for the first time in the big chamber, where their exuviae were found.

The actual process of egg-laying was not observed since it takes place inside an opaque, underground nest. For this reason the date of egg-laying in the field is also unknown. However, one of six females found in winter sand samples laid eggs in laboratory conditions after about two weeks from interrupting its hibernation. About four weeks later spider nymphs emerged from the underground nest. The spiderlings in laboratory performed burrowing behavior and built oval, thin-walled sub-sand nests soon after their first appearing on the surface.

DISCUSSION

The life history analysis suggests, that the lifespan of *Y. arenarius* counted as the time from leaving the sub-sand nests to the last individuals observed in the field is about 720 days for males and 750 days for females (maximum 770 days), which makes it the longest-lived salticid reported from natural conditions (Jackson 1978; Horner & Starks 1982; Matsumoto & Chikuni 1987). There are reports of *Sitticus fasciger*, which lived over 800 days in the laboratory, but only up to 428 days in the field (Matsumoto & Chikuni 1987). From the exceptional variability in the rate of development and lifespan of spiders

(e.g.: Turnbull 1962; Toft 1983) we may expect that the lifespan of the studied spider may also be variable, as local weather conditions and food availability fluctuate.

The life cycle of *Y. arenarius* is characterized by an at least potentially long reproductive period, which may last for about two months in autumn and for another two months the next spring. Copulating spiders were, however, found only in autumn. The possible reason is, that as time elapsed, females were getting less receptive (Bartos pers. obs.) and male condition was also getting worse, especially in spring (Figs. 1–3). Therefore most likely copulation occurred in autumn and egg-laying took place the following spring.

The spiders most probably lay a few large eggs in one batch. Laying multiple batches in the field cannot be excluded, however. Large egg dimensions in comparison to the largest female's abdomen size (Figs. 2, 3) suggest that the total number of eggs laid at one time must be close to the number observed in one batch. Semelparity is also suggested by rather uniform size of spiderlings (at least during the first few months). If there were more than one clutch, they would have to be separated by 1–4 weeks and as a result the spiderlings would differ in condition and size (Horner & Starks 1972; Jackson 1978; Matsumoto & Chikuni 1987), which is not the case here (Figs. 1–3).

Even though the exact period of egg laying cannot be directly indicated, it may occur either in mid April, when female abdomens rapidly shrink or in mid May. At the beginning of this month female abdomens are the largest in the whole life cycle (Figs. 2, 3). No such tendency was observed in average posterior eyes width (Fig. 1), which suggests that the group of measured females did not differ in overall size but only according to their abdomen size. Even though there are two periods when female abdomen shrinks, which may suggest egg laying, the process most likely occurs in May, which is about a month before a new cohort emerged. This is consistent with average period of egg development and nest residence by spider larvae and nymphs (Horner & Starks 1972; Jackson 1978; Matsumoto & Chikuni 1987). The early period of female abdomen shrinking is possibly due to low prey availability, prey becoming more numerous only in late June after juveniles leave their nests (Bartos pers. obs.). Such synchroniza-

tion of egg-laying with food availability has been commonly reported (Almquist 1969; Schaefer 1987). Underground nest location with no signs of repeated nest visiting (Bartos 2002b) imply the lack of brood care.

Life history traits of *Y. arenarius* such as low fecundity and relatively large eggs, slow development, delayed reproduction, long life span and a degree of territoriality (Bartos pers. obs.) place this species as a K-selected organism, well adapted to the unfavorable environment. As one of major predators, outnumbered only by ants (Bartos pers. obs.) it seems to be a successful competitor in the environment. Apart from the spiders' cryptic coloration, the key adaptation to survival in the cover-free habitat seems utilization of underground space, i.e. the burrowing and underground nest building, so typical for many animals dwelling in arid environments (e.g.: Gwynne & Watkis 1975; Cloudsley-Thompson 1983; Henschel 1990). Underground nests provide the spiders with more stable conditions, shelter against night active predators, strong wind and periods of inclement weather such as heavy rains, which may be a severe mortality factor. The importance of the nests is also suggested by the number of nests built especially by juveniles. In the laboratory the juveniles built nests daily, which is significantly more often than in subadults and adults (Bartos 2002b). Such a high rate of nest building in juveniles connected with silk production and apparently energy-demanding underground nest building must be an important expenditure in the energy budget at the expense of other processes, e.g. growth and development.

Morphological and phenological data suggest that the spiders lay eggs two years from the time they hatch. However, in the field, newly hatched spiders are found every year. This suggests that in the dunes of Central and Eastern Poland, there are two sympatric populations of *Y. arenarius* reproducing in odd and even years (Fig. 4). Phenology of males and females in the field suggests that there is no gene flow between the groups or it occurs accidentally and must be limited. Gene flow may take place if adults from one cohort in spring survive until they meet sexual partners from the other cohort in August. This is very unlikely, though not impossible. Males would have to live for another two months and fe-

males for one month longer than the most long-lived individuals in the field. This was not observed in the period of studies since very characteristically looking old females were never recorded after mid July. For females such prolonged survival would also mean to live even longer, for another nine months until the next spring (and hibernate for the third time), when eggs are laid and young were found to emerge from egg sacs.

The apparent reproductive isolation may be, however, incomplete if at least a small proportion of the population reproduces every year or every three years or the immigration from population of an annual cycle (if there is one) occurs. Such phenomena were reported for several spider species (Toft 1976, 1983) and in the recent research on the reproductive isolation of *Araneus diadematus* were the most probable causes of the lack of genetic differences between markedly separated generations (Johannessen & Toft 2002). Another potential cause of gene flow between successive cohorts may be prolonged hibernation or aestivation. However, it seems very unlikely since it would require surviving several months while being immersed in hot and dry sand. The temperature at the depth the nests are built exceeds 50 °C in hot summer days (Bartos pers. obs.). On the whole, no evidence supporting the alternative scenarios were gathered over the period of studies. Interestingly a very similar phenomenon of two sympatric groups isolated by the season of reproduction was described in another salticid, *Sitticus fasciger* (Matsumoto & Chikuni 1987).

It is curious how such a pattern evolved in the first place. Certainly not as a result of the appearance of early and late maturing adults (Schaefer 1987), since we would then find slowly and quickly developing individuals. Instead we observe relatively uniform growth in the whole cohort of individuals.

Two hypotheses seem to be most likely: a) if all populations of *Y. arenarius* require three seasons for development, then a part of them might have been shifted by one season and later mixed with the original group, b) if southeastern populations have shorter cycles, then repeated migrations might have resulted in the pattern observed. Both hypotheses assume two allopatric populations, which possessed cycles shifted from each other by one year. After mixing they formed sympatric

groups isolated by the year of reproduction. Whichever hypothesis is correct, the life cycle pattern we can observe now is probably indebted to the well-known variability of spider rate of development depending on local conditions (Schaefer 1987) resulting in prolonged or shortened cycles (e.g.: Jackson 1978; Toft 1983).

Another interesting question for speculations is: when did it happen? Nowadays this stenotopic species inhabits most commonly well isolated dunes. Ballooning has never been observed and seems an unlikely way of reaching another dune, which is a rare habitat not only in Poland, but in all Europe. Sandy areas were, however, more common in the past. So, did the switch happen as long ago as the time after the last glaciation, when bare moraine sands were common in Central Europe? The author hopes that planned studies will help to test these hypotheses.

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LITERATURE CITED

- Almquist, S. 1969. Seasonal growth of some dune-living spiders. *Oikos* 20:392–408.
- Bartos, M. 2000. Cykl życiowy i strategia polowania pająka *Yllenus arenarius* Menge, 1868 (Araneae, Salticidae). Ph.D. Thesis. University of Lodz, Lodz.
- Bartos, M. 2002a. Distance of approach to prey is adjusted to the prey's ability to escape in *Yllenus arenarius* (Araneae, Salticidae). Pp. 33–38. In *European Arachnology 2000: Proceedings of the 19th European Colloquium of Arachnology*, Aarhus (S. Toft & N. Scharff, eds). Aarhus University Press, Aarhus.
- Bartos, M. 2002b. The sub-sand nests of *Yllenus arenarius* (Araneae, Salticidae): structure, function and construction behavior. *Journal of Arachnology* 30:275–280.
- Bartos, M. 2004. The prey of *Yllenus arenarius* (Araneae, Salticidae). *Bulletin of British Arachnological Society* (in press).
- Cloudsley-Thompson, J.L. 1983. Desert adaptations in spiders. *Journal of Arid Environments* 6:307–317.
- Edwards, G.B. 1975. Biological studies on the jumping spider, *Phidippus regius* C.L. Koch. M.Sc. Thesis University of Florida, Gainesville.

- Gwynne, D.T. & J. Watkiss. 1975. Burrow-blocking behaviour in *Geolycosa wrightii* (Araneae, Lycosidae). *Animal Behaviour* 23:953–956.
- Henschel, J.R. 1990. Spiders wheel to escape. *South African Journal of Science* 86:151–152.
- Horner, N.V. & K.J. Starks. 1972. Bionomics of the jumping spider *Metaphidippus galathea*. *Annales of the Entomological Society of America* 65: 602–607.
- Jackson, R.R. 1978. Life history of *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology* 6:1–29.
- Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. *Annual Review of Entomology* 41:287–308.
- Johannesen, J. & S. Toft. 2002. A test for reproductive separation of alternative generations in a biennial spider, *Araneus diadematus* (Araneae, Araneidae). *Journal of Arachnology* 30:65–69.
- Logunov, D.V. & Y.M. Marusik. 2003. A revision of the genus *Yllenus* Simon, 1868 (Arachnida, Araneae, Salticidae). KMK Scientific Press Ltd., Moscow.
- Matsumoto, S. & Y. Chikuni. 1987. Notes on the life history of *Sitticus fasciger* (Simon 1880) (Araneida, Salticidae). *Journal of Arachnology* 15:205–212.
- Merkens, S. 2002. Epigeic spider communities in inland dunes in the lowlands of Northern Germany. Pp. 215–222. *In* *European Arachnology 2000: Proceedings of the 19th European Colloquium of Arachnology*, Aarhus (S. Toft & N. Scharff, eds). Aarhus University Press, Aarhus.
- Prószyński, J. 1991. Salticidae. Pp. 488–523. *In* *Spinnen Mitteleuropas*. (S. Heimer & W. Nentwig, eds.). Parey Verlag, Berlin.
- Schaefer, M. 1987. Life cycles and diapause. Pp. 331–347. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin, New York.
- Toft, S. 1976. Life-histories of spiders in a Danish beech wood. *Natura Jutlandica* 19:5–39.
- Toft, S. 1983. Life cycle of *Meta segmentata* (Clerck, 1757) and *Meta menzei* (Blackwall, 1869) in Western Europe (Arachnida: Araneae: Tetragnathidae). *Verhandlung des Naturwissenschaftlichen Vereins in Hamburg* 26:265–276.
- Turnbull, A.F. 1962. Quantitative studies of the food of *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). *Canadian Entomologist* 94:1233–1249.
- Vollrath, F. 1987. Growth, foraging and reproductive success. Pp. 357–370. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin, New York.
- Wilcox, R.S. & R.R. Jackson. 1998. Cognitive abilities of araneophagic jumping spiders. Pp. 411–433. *In* *Animal Cognition in Nature: the Convergence of Psychology and Biology in Laboratory and Field*. (R.P. Balda, I.M. Pepperberg & A.C. Kamil, eds.). Academic Press, New York.
- Wise, D.H. 1995. *Spiders in ecological webs*. 1st ed. Cambridge University Press, Cambridge.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall International, Inc., Englewood Cliffs, New Jersey.
- Żabka, M. 1997. Salticidae. Pająki skaczące (Arachnida: Araneae). *Fauna Poloniae*, 16. Muzeum i Instytut Zoologii PAN, Warszawa.

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